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Central routes taken by regenerating optic fibers.

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There is good physiological evidence that regenerating optic fibers of fishes and amphibians find their original place of termination in the optic lobe. Whether the course taken by the growing fibers in regaining their central terminals is a random one or is selective was investigated. Histological studies were made in which section and regeneration of the optic nerve was combined with retinal lesions in goldfish and other species. The results suggest definite preferential selection by the fibers for their original, central pathways: evident in the choice of medial or lateral tracts, in the point of entrance into the tectum, and later, the point of entrance into the plexiform layer within the tectum. Neuronal specificities thus appear to operate in the patterning of fiber pathways of the central nervous system as well as in the details of the synaptic interconnection.

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PERCEPTUAL CAPACITY OF THE ISOLATED VISUAL CORTEX IN THE CAT

BY

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The split-brain approach was utilized in 6 cats to test the degree of functional autonomy in the visual system. The central visual cortex of one hemisphere was isolated by the removal of most of the extravisual neocortex of the same hemisphere. Visual inflow was restricted to the isolated side in four cases by sectioning the crossed optic fibres at the chiasma and masking one eye and in two cases by section of the contralateral optic tract. The isolation produced severe deficits in visual performance, although all cases retained some ability to learn and to recall simple pattern discriminations. The results of two- and three-stage removals of the non-visual cortex, and of terminal section of the callosum, as well as histology of the lateral geniculate nucleus indicated that geniculo-striate damage was not the limiting factor. Removal of fronto-parietal cortex produced as much or more decrement in visual discrimination than did removal of temporal cortex.

INTRODUCTION

It has been found that the somatic cortex is capable of mediating high level perceptual learning and memory in the cat after its isolation by removal of parietal, occipital, and temporal cortex and section of the corpus callosum (Sperry, 1959). The aim of the following was to find out to what extent visual functions might survive similar isolation of the optic cortex. Visual impairments produced by bilateral removal of the frontal eye fields (Fulton, 1955) or the infero-temporal cortex (Chow and Orbach, 1957) suggest the probability of less functional independence in this system. On the other hand, Lashley's findings (1942, 1950) as well as the fibre relations of the striate cortex point to the possibility of a degree of functional autonomy.

The present study involved isolation of the visual cortex of only one hemisphere, the corpus callosum being sectioned and the visual inflow restricted to the same hemisphere. Earlier work has shown that cats and monkeys with midline section of the chiasma and callosum are unable to perform with one eye visual discriminations learned through the other eye (Downer, 1958, 1959; Myers, 1955, 1956; Sperry, 1958; Sperry, Stamm and Miner, 1956). This makes it possible to study the perceptual and mnemonic functions of the isolated visual cortex unilaterally, confining the extensive cortical removals to one side while the other hemisphere is kept intact to prevent paralysis and to serve general background function.

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METHOD

Restriction of the visual inflow to one side was effected in four cases by sectioning the optic chiasma and masking one eye during training and testing following techniques developed earlier by Myers (1955). In two other cases (*Chr*, *Ltm*) it was effected by section of the left optic tract just posterior to the chiasma. The animals were adult cats selected as they became available after serving in other experiments.

The operated animals with vision restricted were taught to perform one of several simple pattern discriminations (see Fig. 1) which were stabilized by overtraining a minimum of 400 trials. Isolation of the central cortical area for vision was then carried out by removal of the surrounding neocortex in one or more stages and by transection of the corpus callosum, the order of the surgical steps being varied in the different cases as described below. Standard surgical precedures were followed throughout. Callosal section was effected by exposure and retraction of the hemisphere opposite the visual area to be tested to avoid damage to the latter. Special effort was made to preserve the larger branches of the middle cerebral artery running to the lateral edge of the isolated cortex.

Training and testing of visual discriminations was carried out by procedures described elsewhere (Sperry, Miner, and Myers, 1955). In brief, the cats were placed in a darkened training box (see Fig. 2) at one end of which were two swinging windows or doors each containing a transilluminated test figure. The test patterns were interchanged from right to left at random and the animals learned to push open the door holding the correct (rewarded) figure. Correct choices were rewarded with morsels of food; incorrect choices were signalled by a buzzer. Tests of generalized visual function were also applied, including visual placing responses, centring and following reactions, avoiding objects in walking, and others as described below.

The brains, following fixation and removal, were checked by gross and microscopic examination. The test hemisphere including the lateral geniculate nuclei was sectioned at 25 μ and stained with cresyl violet. The text figures indicating the cortical removals on a type feline hemisphere are based on examination of the removed brains and on maps drawn at the time of operation. On the medial surface the lesions were continued directly downward to the corpus callosum anteriorly and to the splenial fissure and pyriform lobe posteriorly.

OBSERVATIONS

Removal of non-visual cortex in one stage. In the first case, *Wzl*, the cortical removal was carried out in one stage to the extent indicated in Figure 3. The lateral extension into the auditory region was left intact in this and later cases to avoid damage to the underlying optic radiations. To casual examination the animal appeared to be blind on the affected (left) side during the first two weeks after the cortical removal. It seemed unable to see pieces of food held directly in front of it; it would not jump to the floor from a stool 40 cm. high; and it bumped into objects in walking about a room. Forced circling to the left was pronounced in the first two weeks, more so than in any of the subsequent cases. The tendency to veer to the left had almost disappeared at the end of five weeks. During these first five weeks discriminative performance through the left eye in the testing apparatus failed to rise above chance.

Two months after the cortical removal, *Wzl* had regained the ability to discriminate the light vs. dark patterns L–D. It then relearned discriminations H–V and X–O with no evidence of any retention from the preoperative training. The performance on X–O was erratic, but on H–V *Wzl* attained a consistent performance level of 92 per cent. correct responses.

Section of the corpus callosum four months after the cortical removal again abolished all discriminations up to five weeks after the operation. Beginning with the sixth week after callosal section, discriminations L–D and H–V were relearned a little easier than initially, suggesting some saving. *Wzl* learned further to discriminate a horizontal bar from an upright bar that was tilted from the vertical by stages up to 30°. Beyond this angle the discrimination broke down.

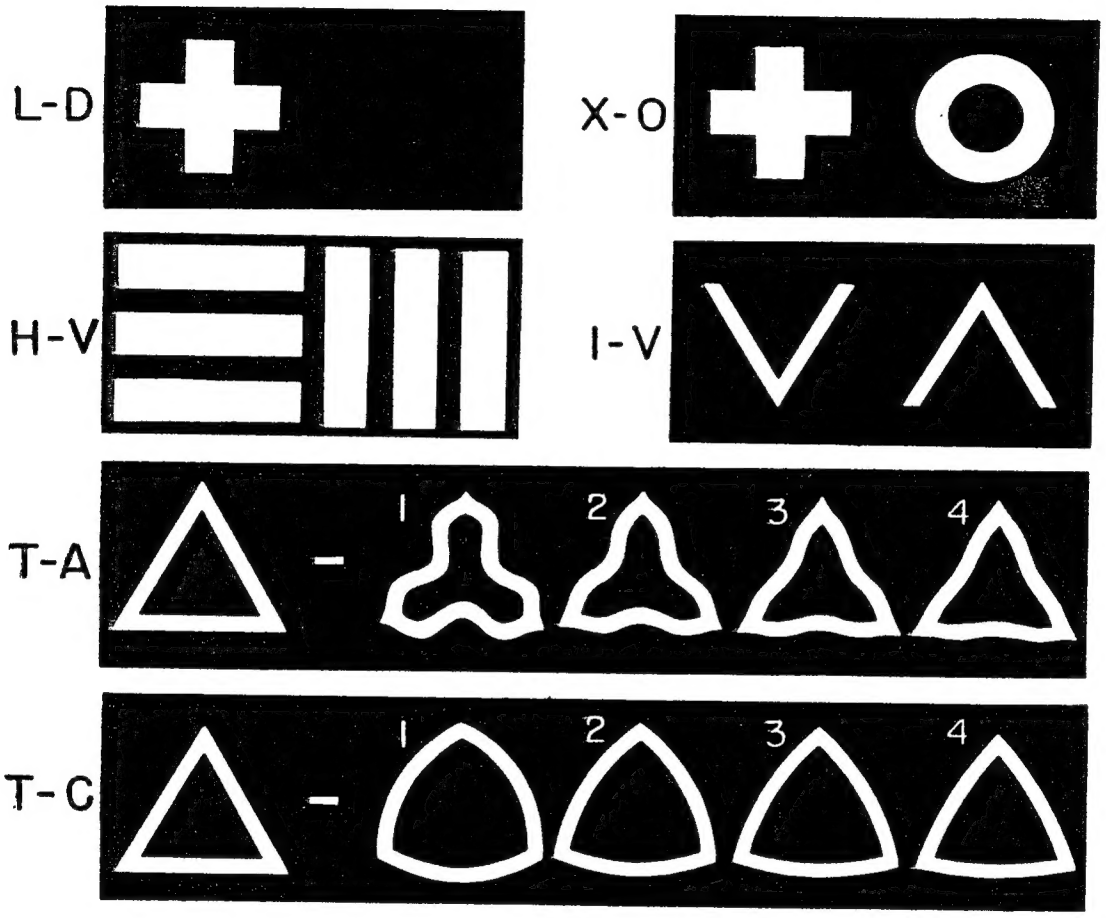

FIGURE 1

Pairs of patterns used in testing visual discrimination. In T–A and T–C only one of the distorted triangle series was paired with the equilateral triangle at left.

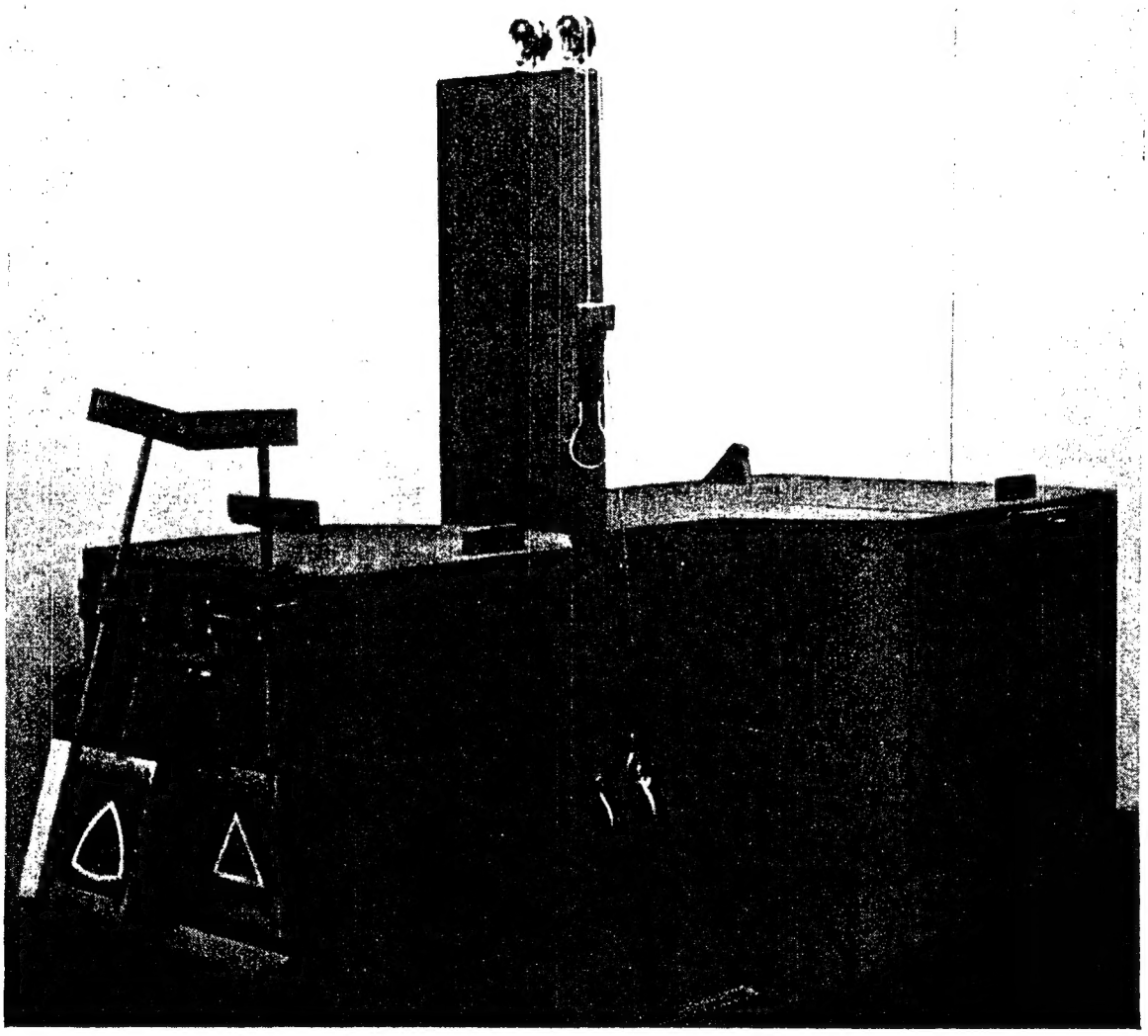

FIGURE 2

Discrimination apparatus. Starting chamber is separated from choice chamber by two sliding doors, one opaque, one transparent.

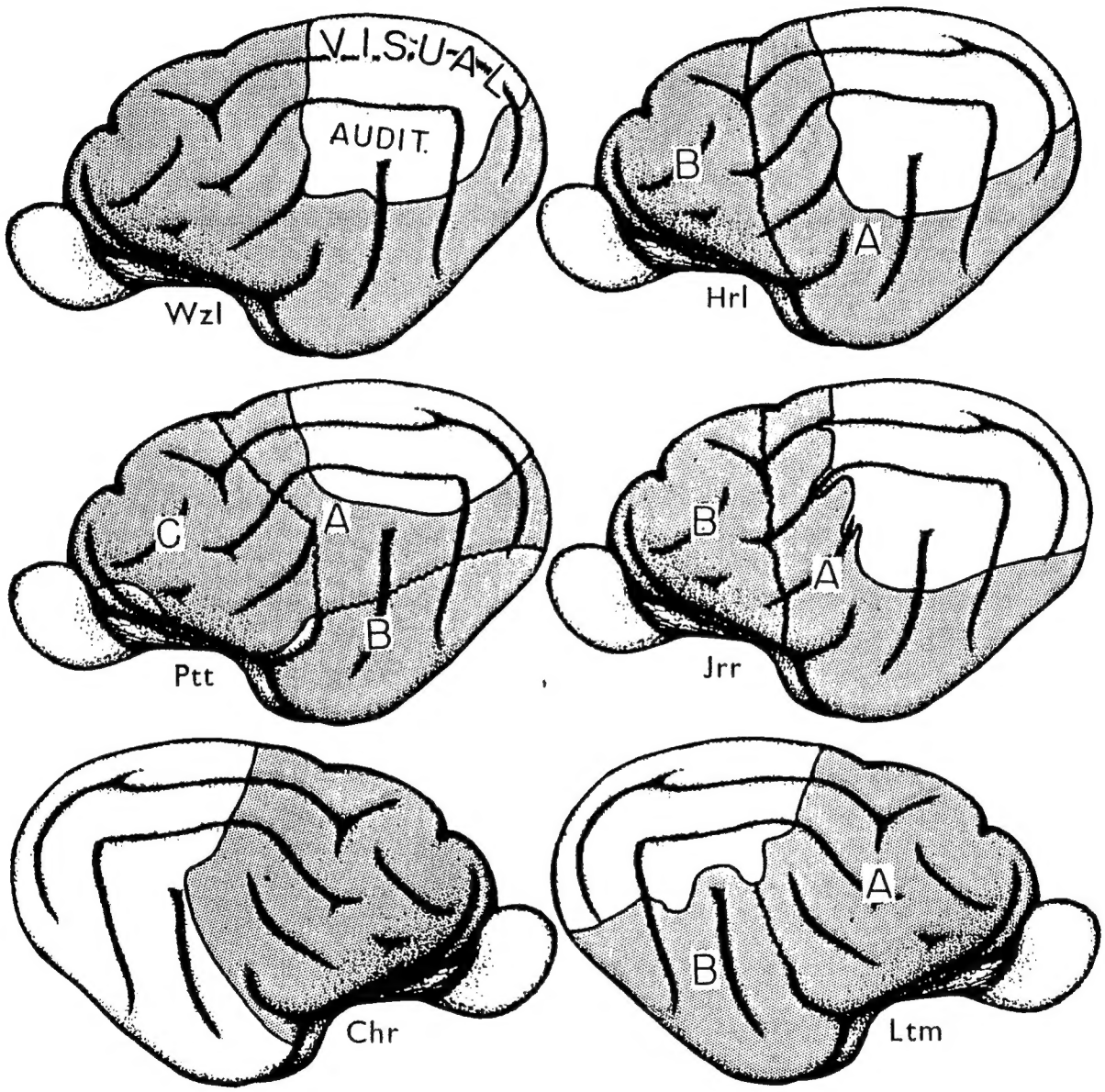

FIGURE 3

Extent of cortical removals (stippled) in test hemisphere. Where the removals were carried out in stages, the order is indicated alphabetically.

In further visual tests with the left eye conducted at three months after section of the callosum we were unable to evoke centring, fixating, or following movements of head and eyes. In walking about an unfamiliar room, the animal bumped into objects directly centred in its path. Visual placing responses were absent as were also the reaching for and striking at small objects. The animal would not jump from one table to another of equal height at 25 cm. distant and balked at jumping to the floor from a low stool. The cat seemed unable to see pieces of meat dangled close in front of its nose. In the discrimination apparatus its performance was very slow and uncertain, and it seemed to tire easily. It would typically run a good series of 9 to 15 perfect runs, then relapse with many errors.

Removal of non-visual cortex in two stages. In the next case, *Hrl*, a wide band of the left cortex bordering the area to be isolated (A in Fig. 3) was removed first so that any damage to the underlying fibre systems would be limited mostly, or entirely to this first stage operation. The preoperatively trained H–V survived this removal with only a transient drop in performance level that was recovered by the 14th day after operation.

On the 18th day following the cortical removal, the corpus callosum was sectioned. During the next ten days the animal appeared blind in the left eye. By the 20th day it was again able to discriminate H–V, and was performing 98 to 100 per cent. correct during the three weeks preceding the final cortical removal. Its visual performance in general remained relatively good.

The remaining frontal region of the left cortex was removed four months after the callosum had been sectioned. This produced an additional impairment of vision, evident both in general tests and in the discrimination box. Beginning 43 days after this operation *Hrl* was again able to discriminate H–V, and like *Wzl*, it learned to distinguish a horizontal bar from one tilted up to 30° from vertical. Other tests of general visual function administered during the 12th week after the final operation yielded much the same results as obtained in the final stage in the preceding case.

Removal of non-visual cortex in three stages. The third case, *Ptt*, was trained to discriminate H–V, X–O, and I–V following transection of the optic chiasm, and the callosal and hippocampal commissures. The first cortical removal involved the area A shown in Figure 3. Discrimination H–V survived with moderately good performance, but X–O and I–V had to be relearned. However, the relearning went rapidly, suggesting partial retention, particularly for X–O.

After consistent performance had been restored on all three discriminations, cortical area B (Fig. 3) was removed 32 days after the removal of A. Discrimination H–V and X–O survived this second removal, but I–V was lost. With retraining, the performance levelled off on H–V at 88 per cent., and on X–O at only 68 per cent. correct.

When the isolation was completed by removal of the frontal region 43 days after removal of B, the effect was much the same as the final stage in the two preceding cases. In the course of six weeks it was possible to retrain H–V and X–O, but not I–V on which there was no sign of improvement after 750 trials. In this final condition *Ptt*, like *Wzl* and *Hrl*, failed to respond visually to food dangled in front of its nose; it walked directly into objects; and in general exhibited much the same picture of visual deficiency as had cases *Wzl* and *Hrl*.

Less drastic removal, two stages. In this fourth case, *Jrr*, the cortical removals were much like those in *Hrl* except that a larger cortical area was left intact (Fig. 3). Particularly the depths of the anterior ectosylvian and suprasylvian fissures were intentionally preserved to avoid damage to possibly important fibres coursing from

the intact cortical area forward into the internal capsule and basal ganglia. In this case the callosum and anterior and hippocampal commissures, as well as the optic chiasm had previously been sectioned and the cat had been trained to perform all the discriminations shown in Figure 1.

The first step in cortical removal involved the area A shown in Figure 3. All the discriminations survived this except I–V, which was quickly restored to the criterion level of 17 out of 20 correct by the 60th trial. Discriminations I–V and T–A3 levelled off at 85 per cent. correct, the others above 90 per cent.

Two months after the removal of A, the remaining frontal neocortex was removed on the same side. Discriminations H–V and X–O were both retained although the performance was much more erratic than before the operation. T–C1 was retained and it was possible to retrain T–C2 but not T–C3. T–A3 was lost but it was possible to retrain T–A2. The performance levelled off between 79 per cent. correct on T–C2 up to 84 per cent. for H–V. The I–V discrimination was lost and could not be retrained.

In the general visual tests this case was somewhat superior to the others. It could centre its gaze on a piece of meat approximately 3 cm. in length held 20 cm. away and could follow the movement of small objects across the middle of the visual field. Visual placing reactions with the left foot were present, though they usually fell short. Unlike the others, this cat seldom bumped into objects in walking an unfamiliar room except when they were approached from the blind half of the visual field.

Visual area isolation with tract section. The experiments were repeated in two additional cases in which the visual inflow was lateralized by section of the left optic tract just posterior to the chiasma. Tract section has the advantage of leaving the crossed as well as the uncrossed optic inflow to the test hemisphere. It also obviates masking one eye during training and testing. In general the visual impairment under these conditions was of much the same order as in the preceding with the following worth special mention.

In both cases the frontal area, labelled A in *Ltm* in Figure 3, was removed first. This produced an impairment as great as or more severe than when the temporal and parietal removals were first. By the third month after this removal the discriminations H–V, X–O, and T–A1 had been recovered to a level of 90 per cent. or better.

The temporal area (B in Fig. 3) was removed in *Ltm* six months after the frontal removal. Beginning eight weeks later *Ltm* again began to perform H–V and X–O and attained levels of 95 and 90 per cent. correct, respectively, by the tenth and eleventh weeks. When the callosum was sectioned in *Ltm* six months after the temporal removal, discrimination was reduced to a level of pure chance for three weeks. Beginning on the 4th week, H–V came back and reached a level of 84 per cent. correct. Three months later *Ltm* was still unable to perform X–O and in the general tests also it displayed a degree of visual defect much like the final stage in *Wzl*, *Hrl* and *Ptt*.

In *Chr* section of the callosum five months after the frontal removal abolished pattern discrimination for three weeks, after which X–O and T–A1 were recovered. However, the performance of these did not rise above 80 per cent. correct during the next three months. The animal continued to perform so slowly and poorly that the temporal removal was not carried out.

Weak centering and following reactions, as well as visual placing, survived in both *Chr* and *Ltm*. Curiously, the callosal section in *Chr* left a pronounced asymmetry in pupillary size—the right pupil being dilated. This was still present, though less

marked, as much as a year later. The pupillary effect was absent or at least much less striking in *Ltm*. All the chiasma-sectioned cases exhibited the lasting bilateral dilation that typically follows chiasma section in the cat.

When the discrimination tests were completed, *Ltm* and *Chr* were used further in a conditioned reflex study (Voneida and Sperry, unpublished). With a flashing light serving as the signal stimulus which was paired with an electric shock to the right paw, it was possible to establish in both cases a conditioned lifting of the right paw to the visual signal.

Anatomical Checks

Examination of the removed brains showed the following: Section of the crossed fibres in the chiasma was complete in *Wzl*, *Hrl*, *Ptt*, and *Jrr*. The left optic tract was also completely sectioned in *Chr* and *Ltm*. Division of the corpus callosum and adjacent psalterium was complete with the following two exceptions: A fine strand of fibres no more than 1·0 mm. in diameter was intact at the posterior edge of the callosum in *Ptt*. The anterior fourth of the callosum was intact in *Hrl*, but it was hardened and presumably degenerate owing to removal of all its cortical connections on the left side.

Examination of right and left lateral geniculate bodies in the chiasma-sectioned cases revealed patches of retrograde degeneration on the isolated side. These degenerate areas were located on the edges, however, and in the cases most severely affected, *Wzl* and *Hrl*, the degenerate areas did not total more than half the volume of the principal dorsal nucleus. Extensive retrograde changes were apparent in the thalamus on the isolated side. The hippocampus, and amygdaloid nuclei were undamaged for the most part as was also the pyriform lobe except for minor invasion of the lateral pyriform area in three cases. On the medial surface most of gyrus proreus was intact in *Jrr*. Smaller remnants of the cingulate and proreus gyri were found on the medial surface in other cases, but no correlation between these and the experimental results was evident.

Discussion

The experiment was undertaken initially on the assumption that directionality in vision is perceived with reference to body posture, especially that of the head and eyes, and hence if all somesthetic cues for posture could be prevented from integrating with the retinal cues, it should have profound effects on visual function. Although the results are in line with this reasoning, they are by no means conclusive.

Removal of the temporal cortex produced no greater, and perhaps somewhat less impairment of vision than did removal of the frontal region. It would appear that the inferotemporal cortex does not play the critical rôle for visual perception in the cat that it does in the monkey (Chow and Orbach, 1957). The nature of the extravisual contribution is quite unknown. The cats acted as if the impairment involved the perceptual process itself rather than its motor expression.

It should be emphasized that survival of the training-box discrimination of the simpler patterns employed in this study is indicative of only a very low level of perception. Even with the entire visual cortex removed bilaterally, the cat may still respond to differences in light intensity and to moving vertical stripes (Smith, Kappauf, and Bojar, 1940). Thus, by using head or eye movements, the cats could conceivably have performed L–D, H–V, and X–O with little use of the isolated area. Actually, head movement did not appear to be used to facilitate the discrimination in this way. Eye movements were not observable.

The visual impairments were not simply a reflection of geniculostriate damage judging from the histology of the lateral geniculate body. The fact that additional impairments were produced by the removal of the distant frontal and temporal lobes after the cortex between these and the preserved occipital remnant had already been removed at an earlier date, gave further indication that the deficits were not attributable to damage either to underlying projection fibres or to circulatory or other secondary damage within the isolated cortex.

The visual deficits were least severe in *Jrr*. The intact cortex that set off this case from the others seemed to be primarily the depths of the anterior ectosylvian and anterior sylvian fissures. This points to the possibility that the cortex here or the fibre systems underlying it have special importance for vision. However, much more analysis will be needed to determine the relative importance of the various cortical areas involved. In general the results point to the probability of several or multiple extravisual factors with a "mass action" type of effect.

In a related experiment in progress somewhat similar isolation of the occipital cortex in a split-brain monkey with sparing of the geniculostriate tract has been observed (Sperry, unpublished) to produce even a greater blinding effect than in the cat.

The transient blindness of one to several weeks' duration produced on the isolated side by section of the corpus callosum was in part presumably a manifestation of diaschisis potentiated by the preceding cortical removals. Diaschisis from major neocortical damage seems in our experience not to be fully recovered before about six to eight weeks in the cat. This fits with the observed period for recovery and enhancement of evoked cortical potentials in areas affected by callosal degeneration (Franklin and Desmedt, 1957). Some of the added impairment produced by callosal section persisted well beyond this period in *Ltm* and *Chr*. This would suggest that sensory or perceptual data were being communicated over the callosum for efferent processing by the more efficient, intact hemisphere.

The visual placing response survived isolation of the visual cortex and the paw preferred was the one contralateral to the remaining somatic area despite the surgical separation of the latter from the receiving visual cortex. This fits with the observation (Schrier and Sperry, 1959) that the split-brain cat can use either paw with equal correctness in learning and performing monocular discriminations.

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3:10. Effects of medial temporal lesions on delayed reactions. R. E. CORRELL AND W. B. SCOVILLE, *Hartford Hospital.*

The effects of bilateral lesions of the medial temporal lobe structures (uncus, amygdala, hippocampus, hippocampal gyrus) on learning and retention of ten-second delayed response (DR) and five-second delayed alternation (DA) were studied in a series of 15 rhesus monkeys. Retention of preoperatively learned DR and DA was not impaired. Postoperative new learning of DR and DA was impaired. There was a more severe deficit on DA than on DR. The deficit on DA was most severe when DR was learned first. Implications for the role of the temporal lobe in memory function are discussed.

3:20. Reversal learning by cats with prestriate and orbitofrontal lesions. HELEN B. WARREN AND J. M. WARREN, *Yerkes Laboratories of Primate Biology.*

Ten normal cats, six with lesions in the suprasylvian gyrus (Prestriates) and eight with lesions in gyrus proreus (Frontals), were tested on 30 reversals of a discrimination habit based on combined visual and positional cues. Both groups of operated animals were significantly inferior to the normal controls on Reversals 1 through 15. The Frontals, but not the Prestriates, were also significantly inferior to the Controls on Reversals 16 through 30. It was concluded that both lesions impair serial reversal learning, but the impairment resulting from orbitofrontal lesions is more persistent. Similar losses in reversal learning are observed in primates.

3:30. Intermanual transfer in split-brain monkeys after somatic cortical ablation. MITCHELL GLICKSTEIN AND R. W. SPERRY, *California Institute of Technology.*

A previous study reported that callosum section tends to block the normally strong intermanual transfer of somesthetic discriminations in monkeys, but that such discriminations may transfer in a minority of cases. To test whether this transfer could be forced by unilateral cortical ablation, two monkeys were used that had previously exhibited no transfer even after extensive overtraining. Somatic arm Area I was ablated unilaterally, and after recovery, subjects were trained to perform new tactile problems and tested for transfer. Both monkeys now exhibited high-level transfer. Results confirm the capacity for intermanual transfer in split-brain monkeys and suggest mediation via ipsilateral somesthetic projections.

3:40. Delayed object-quality discrimination in hemicerebrectomized monkeys. DONALD C. KRUPER, ROBERT A. PATTON, AND YALE D. KOSKOFF, *University of Pittsburgh and Montefiore Hospital, Pittsburgh, Pennsylvania.*

Five hemicerebrectomized and five normal monkeys were tested on a delayed object-quality task (DOQ), using randomly presented intertrial delays of 20, 40, 80, and 120 seconds. Although the normal subjects performed significantly better on the overall scores, significant group differences occurred on only 40- and 80-second scores. Separate interval scores, within the same groups, showed the following relationships to the 20-second scores: (*a*) lower performance on all longer intervals by the operated group and (*b*) lower performance on only the 120-second interval by the normal group. DOQ performance was lower as a function of the delay variable, more for the operated than for the normal subjects.

3:50. Simultaneous learning of two conflicting problems by split-brain monkeys. COLWYN B. TREVARTHEN, *California Institute of Technology.* (Sponsor, Roger W. Sperry)

It has been shown that conflicting visual discrimination habits can be established in right and left hemispheres of the split-brain monkey (corpus callosum, optic chiasma, and anterior commisure cut) by seriatim or concurrent training of separate eyes. Polarized light techniques were here employed to test if the two separate and opposing discriminations could be learned simultaneously, i.e., with each trial contributing to the learning in both hemispheres. Superimposed patterns of polarized light were back-projected on two plastic screens viewed through polarizing filters, one for each eye, oriented at right angles to each other. Results show a tendency for one dominant hemisphere to learn at the expense of the other, but in some cases there is indication that both learn simultaneously.

4:00. The effects of hemicerebrectomy on the solution of the oddity problem by monkeys. STEPHEN A. KUSHNICK AND CARL E. WEDEKIND, *Montefiore Hospital, Pittsburgh, Pennsylvania, and the University of Pittsburgh.*

Four object-quality trained hemicerebrectomized rhesus monkeys were trained in the standard oddity procedure, in order to evaluate the effects of this operation on the "abstract" abilities in monkeys. The data demonstrated that hemicerebrectomy produced no significant impairment in oddity learning. Descriptive comparisons of the data with that of normal monkeys and other brain lesion groups demonstrated that performance by hemicerebrectomies was similar

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